
Chapter III

The Neuropsychology of Attention: Emotional and Motivational Controls

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I. Introduction

Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought.

—W. JAMES (1890)

William James, in *The Principles of Psychology* (1890), began his discourse on attention with this straightforward description of what is now called selective attention. He then went further in the chapters on attention and the will, to outline at least 12 attentional modes of operation. His analysis anticipated most of the current theory, as well as describing certain phenomena that have yet to be considered or studied. Thus, anyone willing to dip into *The Principles of Psychology* will find a clear statement of the ranges of behavioral manifestations of "paying attention." However, James was unable to solve the problem of **how** attention is paid, and had no evidence available to him concerning the mechanisms involved in the control of attention, the problems which form the content of this paper. Before outlining the current evidence on control mechanisms in attention, it is of interest to follow the historical

events that led to the rebirth of attention as a valid concept in psychology. Attention has returned through the backdoor, as it were, and has appeared in different guises depending upon the specific orientations of the various investigators.

Experimenters measuring animal behavior were forced to admit the importance of "attention" when animals were found to notice some stimuli and ignore others in studies on cue sampling and discrimination learning (Trabasso & Bower, 1968; Honig, 1970). These experimenters explained their data in terms of cue salience, assuming that certain stimulus parameters were more noticeable or meaningful to the animals. Human experimental research has focused exclusively on selective attention. Studies were initiated in an attempt to answer the question posed by Miller (1956) and Broadbent (1958) concerning how a limited central processor reduces the flow of information received from the senses. The impetus to this line of inquiry stemmed from information theory. Selective attention research has spawned subsets of inquiry such as "divided attention" research utilizing dichotic listening techniques (Treisman, 1969; Kahneman, 1973). Speed or efficiency of the selective process, measured in reaction time, has also been of considerable interest to experimenters using visual and auditory search tasks (Kornblum, 1973). Neisser (1967) in his book on cognitive psychology attempted to frame categories of attention by suggesting that attention operated selectively in two primary modes. One was broad, unfocused, and extracted global information; the other was narrowly focused and permitted detailed analysis. In either case, memory traces of previous perceptual events feed out (MacKay, 1956; Pribram, 1971) to operate upon the incoming stimuli, a process he called "analysis-by-syntheses" His definition is synonymous with what James had described in 1890 as "pre-perception," a process concomitant with paying attention. Thus, the behavioral sciences have begun to map a range of phenomena which are subsumed under the headings of selective attention and discrimination.

Meanwhile, investigators in the brain sciences and in human psychophysiology have been converging, through quite disparate experimental techniques, on the concept that attention varies as a function of arousal or activation, terms often used interchangeably to describe a continuum from wakefulness to sleep. Because arousal and activation are central to the theoretical framework developed in this paper, we will pursue the historical course of this discovery in some detail.

In the 1920s Berger reported that during changes in wakefulness, brain waves recorded from the scalp (EEG) could range between fast, low voltage activity and the slow, high amplitude wave forms characteristic of deep sleep. The physiological correlates of these shifts of activ-

ity remained a mystery until the discovery by Lindsley, Bowden, and Magoun (1949) and by Moruzzi and Magoun (1949) that the reticular formation, a collection of short-fibered, many branched neurons in the brainstem, is essential for maintaining an alert organism. Lesions to portions of this system caused somnolence, coma, and death, whereas electrical stimulation of these same regions produced an alert organism with fast brain wave activity.

These results, along with others, served to initiate a conceptualization of the brain as "aroused" or "activated." Allying these discoveries to the behavioral data on performance efficiency during different intensities of stimulation, researchers began to view both brain and behavior as complying with the Yerkes-Dodson law (1908), which postulates an inverted U-shaped function of efficiency depending upon the degree of "arousal" of the organism. Under or overaroused subjects perform poorly; optimal efficiency occurs in a moderately aroused state (Hebb, 1955). The activity of the reticular formation was assumed to parallel these states. Thus far, no EEG correlates of "overarousal" have been demonstrated.

The notion of brain activation or arousal as existing on a continuum has led to a considerable amount of confusion in the light of subsequent investigations. This confusion has been particularly evident in human psychophysiology in studies of emotion where changes in autonomic nervous system (ANS) activity have been produced by psychically arousing events. Paradoxes soon became evident. The desynchronization of the EEG corresponded to many of the peripheral changes, yet gross EEG does not habituate readily to stimulus repetition, whereas autonomic responses do so reliably. Critical experiments by Lacey (1967); Lacey and Lacey (1970) challenged the notion of a unified arousal mechanism by demonstrating a fractionation in responding between physiological systems. When a subject looks or listens to external events, heart rate slows and skin resistance decreases. However, when a subject attempts to solve a difficult problem, heart rate accelerates rapidly, while skin resistance still decreases. (This same phenomenon was observed by Feré in 1899.)

Additional problems for a unified arousal theory were produced by the concurrent endeavors of Sharpless and Jasper (1956) in the United States and Sokolov (1960, 1963) in Russia. These researchers originally discovered that when arousal to a novel event produced a change in the activity of the CNS and ANS, habituation of the response will ensue if the event is recurrent. Sokolov went a step further, however, by showing that changing any parameter of the stimulus causes a reappearance of the arousal response, or in the Russian term, the orienting reflex. This suggests that the arousal reaction may reflect a mismatch of novel input

to a brain representation of prior inputs—a “neuronal model.” Sharpless and Jasper also noticed that the CNS response separated into a *phasic* component which habituated readily and a *tonic* component which habituated more slowly. Studies have demonstrated that the phasic portion is almost always on the order of 1–3 sec, depending upon the intensity of the stimulus, and is essentially reflexive. It is most commonly produced by a mismatch to a previously encoded input (a memory trace). In other words, it suggests that the phasic portion of the orienting reflex is sensitive to stimulus information. The balance between the phasic (orienting) and the tonic portions can be brought under voluntary control and depends upon the interest or intentions of the individual. Note that arousal seems to split into two parts, one of which is partly outside the control of the subject, and one which is not.

A final blow to the unified arousal concept came from the results of lesion studies on humans and on monkeys by Pribram (e.g., Bagshaw, Kimble, & Pribram, 1965; Kimble, Bagshaw, & Pribram, 1965; Luria, Pribram, & Homskaya, 1964). It was found, contrary to expectation, that the behavioral correlates of orienting (head turning, ear flicking, focusing, etc.) could be dissociated from the autonomic responses of skin resistance and heart rate. The critical finding was that if the organism failed to produce autonomic responses to stimulation because of specific lesions, behavioral orienting was observed, but the behavior failed to habituate. The brain structures involved in this dissociation were the frontal cortex, and the amygdala (a system of basal nuclei found in the forebrain).

It will be apparent from these studies that a unitary arousal concept is too simplistic, forcing the conclusion that more than one process is involved. The hope of arriving at principles relating arousal to attention seems at first glance even more elusive. Already we have touched upon a vast range of processes: arousal, activation, and habituation; stimulus facilitation, cue salience, etc. How can these possibly relate to selectivity, discrimination, analysis-by-synthesis, and global and focused attention?

The distinction noted by Sharpless and Jasper between phasic and tonic arousal provides the key to a possible solution. James initially drew a similar distinction when he referred to two major categories of attention. He noted that certain classes of biologically relevant stimuli which are novel, salient, or intense impinge upon awareness regardless of ongoing activity. Further, he observed that there are modes of attending in which the subject determines the contents of his own awareness and the duration of each episode. He called the former involuntary or *reflex* attention, and the latter voluntary attention, or the *will*.

II. Arousal, Activation, and Effort—A Model of Attention

In our review on animal and human neuropsychology and psychophysiology (Pribram & McGuinness, 1975), this division became the cornerstone of a model of attention. At present, we find the edifice intact and the model strengthened and amplified by new data, especially from recent biochemical evidence on brain systems. We wish to restate our original model, to elaborate our rationale, and to include new data which provide an unequivocal basis for our original suggestion of three major systems that operate as controls on attention.

The distinction between involuntary and voluntary attention identifies two aspects of attentional control. To bring these concepts into line with the evidence and the terminology from physiological studies, the involuntary modes have been redesignated as *arousal*, a phasic short-lived and reflex response to input, and *activation*, a tonic long-lasting and involuntary readiness to respond. A third system coordinates arousal and activation. The operation of this system results in voluntary control and is experienced as *effort*.

Note that the model refers exclusively to **process** and not to the **content** of awareness. Much of the difficulty in establishing a viable framework for the categories of attention has been caused by the confusion between state, process, and content. This confusion is amplified by the resurgence of interest in consciousness. Consciousness has been used interchangeably with awareness, and with attention. Because of this confusion, we wish to draw careful distinctions between the way we intend to use psychological language.

Consciousness, which will not be a topic for discussion in this chapter, infers a *state*. The state of consciousness results from the sum or interaction of all possible neurochemical events affecting it. (For a more detailed account of consciousness, see Pribram, 1976). We accept for purposes of this paper that the controls on attention operate concurrently during a state of consciousness best described as normal wakefulness.

Further, these mechanisms controlling attentional set are independent of the perceptual and ideational contents of awareness (the "one of several possible objects" James described). A more formal description of this interaction is that each state of consciousness can invoke several modes of attention, each of which requires a particular configuration of the arousal, activation, and effort systems. These modes operate on the contents of awareness to define a bounded set, one of a number of possible sets. What is selected is determined either by sudden or intense

stimuli, or by previous perceptual and motor experiences and their associational memories. The sensitivity of discrimination or the speed of selectivity in a reaction time task may be constrained less by attentional control than by the efficiency of the perceptuo-motor apparatus.

Our model thus deals with the physiological systems that operate the attentional controls on perceptual events and not with perceptual events themselves or transformations (cognitive operations) on these events. These distinctions must be kept clear because different brain systems are involved in attention, perception, and cognition. The interaction between these systems is another problem for the study of attention and one that will be touched upon only briefly in this presentation.

A. Arousal

It has been noted that the ubiquity of the arousal concept has obscured more than it has enlightened. Here we restrict the use of the term to be synonymous with the orienting reaction.

Arousal is said to occur when an input change produces a measurable phasic change in a physiological (e.g., GSR) or behavioral (e.g., head turning) indicator over a baseline. The types of input change that produce arousal have been studied extensively and have been labelled by Berlyne (1969) as collative (defined as, to collect and compare carefully in order to arrange into informative order) variables. These include sudden changes in intensity to which the organism is unaccustomed, changes in the timing of inputs, and changes in the ground in which a stimulus figure appears. In short, arousal results when, in the history of the organism's experience, an input is surprising, complex, or novel. Such collative characteristics also define the concept "information" as it is used in the study of communication systems (e.g., Brillouin, 1962); thus it has become customary to treat organisms subject to arousal as "information processing systems." Inherent in such treatment is the assumption that the input is matched against some residual of past experience in the organism, or some competence (Bruner, 1957; Miller, 1960; Pribram, 1971). Without such matching, there could be no novelty or information, nor even a measure of change in intensity.

It was noted previously that the waning or habituation of the arousal response must be due to the establishment of such a residual neuronal model of that event—since any small change in one parameter of the signal will reconstitute the arousal reaction (Sokolov, 1960, 1963). Further, certain salient stimuli, such as one's name, produce facilitation and not habituation, at least in a relevant context, suggesting that a high-

level override is involved. We note therefore that there are two consequences of the orienting reaction; reflex behavioral and neural changes over baseline, and mnemonic "registration" which ensues with stimulus repetition.

B. Activation

The interaction between behaving organisms and their environment is not one-sided. The organism is not a switchboard for incoming stimulation. Rather, behaving organisms are spontaneously active, generating changes in the environment often by way of highly programmed (i.e., serially ordered) responses (Miller et al., 1960; Pribram 1960, 1962, 1963, 1971). These organizations of behavior must involve the construction of neuronal models in at least two ways: (a) control of the somatomotor system which effects the responses and (b) feedback from the outcomes (reinforcing consequences) of the behavior. Sherrington (1955), in discussing central representations, framed the question: "Is the organism intending to *do* something about the stimulus variables in the situation?" Germana (1968, 1969) in a review of the evidence, suggested that any central representation or neuronal model must include such "demand" characteristics. Thus he proposes that Pavlov's "What is it?" reaction (which we have called arousal and the registration of input in awareness and memory) may not occur in isolation from a "What's to be done?" reaction. As we shall see, our analysis suggests that both reactions occur and that they can be distinguished: arousal and the registration of input indicating "What is it?" and readiness signaling "What's to be done?"

Activation differs from arousal therefore in maintaining a set to continue ongoing behavior. Maintaining a tonic readiness is reflected in an increase in cortical negativity (CNV) (e.g., Walter, Cooper, Aldridge, McCallum, & Winter, 1964; Donchin, Otto, Gerbrandt, & Pribram, 1971) and tonic heart rate deceleration (Lacey & Lacey, 1970). Studies of readiness have shown that with development an additional component comes into play. This component is "vigilance" and is addressed to overcoming habituation in situations in which the maintenance of a set is no longer automatic.

C. Effort

Thus the systems involved in arousal and activation can be distinguished; arousal defined as a phasic reaction to input; activation, as a

tonic readiness to respond. Yet, under many circumstances, the two reactions appear to be yoked. In such situations they share the function of reflex coupling input to output, stimulus to response. In the absence of controlled arousal and activation, behaving organisms would be constantly aroused by their movements and moved by arousing inputs. There must be some control process that involves both arousal and activation and allows the uncoupling to take place. Manifestations of this process are registration and its consequent habituation and the overrides on habituation, such as facilitation and vigilance. As a rule, action generated inputs (the outcomes of actions—their reinforcing consequences) appear to generate more complexly structured neuronal models than repetitions of simple inputs. This complexity is largely the result of participation of the central motor systems in generating input. Thus it takes longer to form a habit in, than to habituate to, the same situation. Such a process, requiring flexible shifts from a change in primitive through-put states, appears to be experienced as effort.

Effort is reflected centrally (see last section) and peripherally where muscular contraction shifts to an anaerobic metabolic cycle (Berdina, Kolenko, Kotz, Kuzetxov, Rodinov, Savtechenco, & Thorevsky, 1970). This is particularly noticeable during problem solving and is accompanied by chronic accelerations of heart rate (Lacey & Lacey, 1970).

Effort is thus defined as an expenditure of energy (metabolic output) due to a change of state in central control systems. This definition is in keeping with a physical definition of energy (e.g., McFarland, 1971) as the capacity for doing work, that is, for changing the state of a system. Effort then, is a measure of the *rate* of changing the state of a system (or maintaining a state in the face of changes in external parameters).

III. Human Psychophysiology and Autonomic Correlates of Attention

A. Arousal

A major departure from the concept of a unified arousal model initially stemmed from Sharpless and Jasper's (1956) designation of phasic and tonic arousal. Once the implications of this division became clear, a host of human psychophysiological data fell into place. The notion of effort further clarified the significance of heart rate elevation.

In studies measuring changes in autonomic activity (skin conductance or GSR, blood pressure, heart rate, etc.) while the subject is paying

attention, the sympathetic nervous system measures (GSR or blood volume) often mirror stimulus parameters of novelty and complexity, whereas the parasympathetic division controlling the vagal regulation of heart rate, reflects the parameters of the somatomotor readiness and response mechanisms—which in turn reflect the incentives and response biases developed as the reinforcing consequences of behavior. This distinction has been clearly demonstrated in studies by Elliott (1969), Elliott, Bonkart, and Light (1970), by Dahl and Spence (1971), and by Hare (1972).

Experimenters appear to use the term arousal defined by the amount of information in the stimulus, and studies of selective attention in which input must be categorized by the subject before he can respond appropriately have shown consistently that sympathetically innervated phasic responses distinguish between variations in task largely on the basis of their novelty, surprisingness, or complexity (Blaylock, 1972; Hare, 1972; Kilpatrick, 1972; Lacey & Lacey, 1970; McGuinness, 1973). A typical experiment (Hare, 1972) in which subjects viewed slides without discriminating between them were less aroused (showed fewer skin conductance changes) than those who had to categorize. Differences in phasic skin conductance amplitudes and these phasic responses returned to baseline (habituated) over trials. Difficulty due to changes required in response operations were reflected in tonic skin conductance; most precisely by tonic heart rate changes.

A precise relationship between tonic levels of skin conductance and response output variables has not been demonstrated. To date, skin conductance has not been implicated in any metabolic function (Venables & Christie, 1973), but data by Bohlin (1976) suggest that either readiness (state of activation) or effort produces a elevation in tonic skin conductance. In her study, subjects were asked to perform difficult mental arithmetic tasks interspersed with habituation trials to a series of tones. Skin conductance was continuously and significantly elevated in both shock-threat and no-shock-threat groups compared to controls who relaxed throughout the experiment. Bohlin describes these groups as exhibiting tonic "arousal." We would suggest that the experimental groups were maintaining readiness to respond to the arithmetic problems and that this required effort. However, more information is needed to understand how tonic skin conductance levels relate to the parasympathetic activity that produces tonic heart rate changes. Current data show that the involvement of somatomotor responses during activation or readiness affect tonic cardiovascular changes, and this relationship provides one clue to unraveling the controversial and apparently dispa-

rate views of the psychophysiological mechanisms involved in attention. We therefore focus on the relationship between heart rate, the somato-motor readiness system, and effort.

B. Readiness and Execution

Two prevailing theories concerning the meaning of cardiovascular processes during attention appear diametrically opposed. On one hand, there is the baroreceptor feedback theory of Lacey (1967); Lacey and Lacey (1970) which, simplified, states that increased heart rate will directly affect stimulus intake or rejection through a process of feedback to the bulbar inhibitory centers in the brainstem, reducing arousal of the central nervous system (Bonvallet & Allen, 1963). On the other hand, Obrist and his colleagues (Obrist, Webb, Sutterer, & Howard, 1970a,b) propose that heart rate is regulated by the motor demands of the organism that are controlled centrally. Findings by Jennings, Averill, Opton, and Lazarus (1971) have challenged the adequacy of either of these explanations and have produced results in line with an "amount of attention" hypothesis. They argue that as demands on attention increase, heart rate will **fall** in proportion to the number of the categorizations demanded by the task, unless metabolic activity is engaged. This is somewhat in line with the view of this article, but their suggestions are still incomplete. As they note, this hypothesis does not explain the functional significance of cardiac deceleration during attention. Nor, we might add, does it explain why heart rate always **increases** during problem solving.

To resolve these conceptual difficulties, the physiological processes will be examined in more detail. The assumption of a majority of theories is that there is a unitary relationship between cardiovascular and somatic processes, whereas evidence shows that the situation is far more complex (Lawler, Obrist, & Lawler, 1976; McCanne & Sandman, 1976).

Any registered orienting response produces a dual sympathetic-parasympathetic effect. The cardiovascular reflex in orienting results in sympathetically controlled and cholinergically mediated gross blood flow shifts which are sometimes accompanied by an initial phasic heart rate acceleration. This will vary in magnitude with stimulus intensity (Graham & Clifton, 1966), and an initial respiratory block will often combine to elevate the acceleratory effect (Jennings et al., 1971; Petro, Holland, & Bouman, 1970; Wood & Obrist, 1964), although the effect of intensity is not entirely predictable (Bull & Lang, 1972). We now know that this is due to parasympathetic inhibition, and that all attentional (as

opposed to movement-produced) heart rate changes are under vagal regulation (Eckberg, Fletcher, & Braunwald, 1972; Forsyth, 1970; Obrist, Howard, Lawler, Sutterer, Smithson, & Martin, 1972).

The initial arousal phase is followed immediately by a heart rate change in the direction of deceleration, which is due to the vagus re-stabilizing the system. If the prepared somatic systems become mobilized to initiate an appropriate consummatory or defense pattern—eating, drinking, withdrawal, flight, or attack (Abrahams, Hilton, & Zbrozyna, 1964)—heart rate will then come under the control of the somatomotor system and a chronic increase in rate occurs to meet the demands of the activity. The processes occur in fixed order: Stimulus → blood flow shift → heart rate acceleration → heart rate deceleration, until the motor response determines tonic heart rate acceleration and the system ultimately restabilizes.

During a vigilance or categorization task involving the prolonged intake of information (Lacey & Lacey, 1970), the vagal restabilization phase is extended as part of a tonic activation—the vigilant readiness process. Lewis and Wilson (1970) examined cardiac responses to a picture-matching task in young children. In all children, a marked deceleration occurred which lasted until the choice was made. The most interesting finding was that the greatest deceleration was related to correct responses—if a subject was asked to guess again, heart rate did not return to baseline until the final choice. Correct responses occurred with longer response times and greater cardiac deceleration, which supports the suggestion that the vigilant readiness phase of the control processes has been extended.

Correlation with IQ demonstrated that there was a relationship to both deceleration and error score for girls only. The sex difference finding could possibly be due to the greater amount of movement found in boys, which would cause a heart rate acceleration and less attention to the task. This explanation is made more tenable by the recent finding of Obrist, Howard, Sutterer, Hennis, and Murrell (1973) that children's reaction times are slower in proportion to the amount of uncontrolled movement they produce. The relationship between motor control and reaction time was linear with age. As reaction times increased, motor responses and heart rate decreased. We therefore suggest, in line with Obrist et al. (1970a,b), that when activation must be maintained, heart rate deceleration occurs as an accompaniment of somatomotor readiness.

This then partially accounts for the sequence of physiological events occurring when the organism prolongs attention while categorizing external events. During this intake episode, he reduces extraneous noise

by eliminating random movements. Heart rate adjusts to the reduced demands of the system, reflecting characteristics of the somatomotor system in which overt movements regularly precede blood flow changes and heart rate acceleration. For example, Petro et al. (1970) found that after a voluntary contraction of the biceps muscle, heart rate increased with a latency of approximately 500 msec. However, when problem solving, with its emphasis on which response to produce when, and the actual trial-and-error making of overt or covert responses is initiated, the cardiovascular and somatomotor response relationship is reversed.

C. Muscular Effort and Problem Solving

The locus of the demand for effort is different in categorizing and in problem solving or reasoning, and this raises the question of (a) the relationship between the various forms of attention and effort, and (b) the nature of effort itself. Could it be that the muscular contractions involved in making responses are totally responsible for the effort necessary in problem solving? A change in actual movement as during categorizing and reasoning would obviously be accompanied by a decrease (categorizing) or an increase (reasoning) in isotonic contraction, but, activation of the readiness mechanism may also be due to change to a special sort of metabolism, usually thought to be largely anaerobic, which has been shown to be active during concentration and problem solving, and which involves isometric contraction.

An understanding of this special metabolic process during attention has been provided by Berdina et al. (1972). Until this study there was no functional explanation for the finding that sympathetically innervated blood flow shifts actually reduce oxygen uptake by the muscle, whereas somatic activation increases it (Rosell & Uvnas, 1962). The study of Berdina et al. (1972) suggests the possibility that this special sort of metabolism of muscle fibers is due to cholinergic mediators. Berdina et al. were interested in the effect of problem solving on blood flow and muscle contraction. They were the first to establish any precise relationship between electromyogram (EMG) recording and problem solving due to the small amount of amplification produced by the technique, which often results in unreliable values (Jennings et al., 1971; Lader, 1965; Matthews & Lader, 1971; see also McCanne & Sandman, 1976). To avoid this difficulty, they introduced a condition of partial muscular contraction: Subjects had to grip a hand dynamometer which they were pretrained to maintain at 30% of their maximum grip. Then, during the problem-solving experiment, subjects were asked to grip the dynamometer for as long as possible.

Both contraction alone and problem solving (arithmetic) alone caused significant blood flow changes. However, a combination of contraction plus arithmetic produced no greater changes in blood flow than either condition alone. On the other hand, the contraction **duration** was significantly increased by arithmetic from 181 to 235 sec ($p < .001$). To disentangle voluntary effects from purely reflex effects, they induced a forearm contraction by electrical stimulation. The results were the same even when the subject had no voluntary control over his muscles. An injection of atropine significantly decreased blood flow during arithmetic, and during contraction plus arithmetic, but not during contraction alone. Atropine also reduced contraction duration during the combined task, showing that the increased contraction during problem solving was **not** a somatic effect since small amounts of circulating atropine do not affect the neuromuscular junction. It was concluded therefore that some form of sympathetically controlled metabolism was causing muscle force to increase, making muscles "work" under the special conditions of isometric contraction.

Apart from other considerations, this experiment demonstrated conclusively that muscular effects do occur during problem-solving tasks and that they involve gross changes in tonicity which cannot always be observed by EMG recording. Equally relevant is the fact that as heart rate correlates so precisely with blood flow changes (Matthews & Lader, 1971), an increase in blood flow during problem solving automatically implies a corresponding increase in heart rate. The Berdina experiment thus explained the functional significance of heart rate changes during problem solving and reasoning: Maintaining attention while problem solving is effortful and involves hard work and hard work is accompanied by metabolic changes. The results of this study appear to establish the outlines of the metabolic processes operating during intense concentration.

In summary, the discovery that two types of muscle activation (isotonic and isometric) and two metabolic functions (aerobic and anaerobic) are involved in both voluntary (effortful) attention and action makes it easier to understand why some confusion has arisen in the study of the psychophysiology of attention. Returning briefly to the Lacey hypothesis, physiological responding during stimulus intake will depend entirely upon how a task is constructed and whether it is primarily a categorizing or reasoning problem. We agree with Lacey that during a state of behavior characterized by heart rate deceleration, we are most open to environmental cues (Lacey & Lacey, 1970) but not necessarily for the reasons he suggests (see also a critique by Hahn, 1973). Lacey's theory also requires acceleration when decisions are made.

How then could one interpret what is occurring during the acquisition of a perceptual or motor skill? When the coordination of arousal and activation is demanded, heart rate acceleration reflects the amount of effort involved in registering, adjusting, and changing the central representation to the requirements of the task. In accord with Lacey's assumptions, intake of information may alternate with concentration. A process ensues that must constantly shift among relevant stimuli in order to overcome the rapid decrementing of the system (just as continuous eye movements overcome the rapid adaptation of retinal receptors). When one plays tennis, for example, heart rate is elevated, but the player must flexibly attend (be aroused by) such cues as the angle and velocity of the approaching ball, the ground lines, the height of the net, and the position and angle of the opponent's body and racket. The intricacy of the series of highly refined changes in response and the transformational calculations based on this evidence could elevate heart rate, even without the behavioral activity of playing tennis (e.g., in a spectator). This is brought out clearly in a study by Johansson and Frankehauser (1973) in which high heart rate accompanied the complex transformations required during an intake task.

In reasoning tasks, activation precedes arousal. For instance, in playing a game of chess or engaging in any similar pursuit requiring transformational calculations, reasoning must occur before the effective response. Once the "move" has been made, it may arouse an "aha" reaction: The move was successful, or, "Oh dear, why didn't I see that!" Again, the physiological changes that occur are those that have been shown in the Berdina experiments, although the theories of Jennings et al. (1971) and Obrist et al. (1970a,b) would predict the opposite.

Some of the task variables which affect arousal and activation and the effort required to overcome resistance to extinction of a prior set during categorizing and reasoning have also been investigated by Dahl and Spence (1971). They propose an activation theory which adopts Bergum's (1966) technique of taxonomic analysis of performance, in which tasks are evaluated according to complexity and activation of response. Task demands were rated by independent judges, and the amount of heart rate change was correlated to each task. Heart rate increased with response demand, and all correlations were significant. A subsequent factor analysis revealed a major factor which they designated "density," or degree of concentration required; in other words, the total amount of cognitive **effort** involved in the task. The other factor which accounted for the greatest amount of variance in task performance was information content of relevant stimuli. Thus, again, collative variables were distinguished from the amount of transformational effort or "work" required in problem solution.

In summary, the autonomic changes that take place during processing of external and internal events appear to be consistently or lawfully related to certain attentional modes. Any sudden or informative input triggers an arousal response which is reflected most precisely by phasic responses of the sympathetic nervous system. When an organism is maintaining a set to respond to externally produced events, heart rate deceleration is generally observed. Conversely, when problem solving takes place, typified by what Lacey describes as a stimulus rejection episode, heart rate acceleration reflects the amount of effort required by the task in uncoupling the involuntary arousal-activation systems.

IV. The Delineation of Brain Systems in Attention

A. The Control of Arousal in Reflex Attention: The Corebrain Arousal System and the Amygdala Circuits

Just as arousal produces a phasic response of the sympathetic nervous system, studies of the behavior of neural systems during arousal in animals have revealed that phasic responses to sudden changes in stimulus events are a ubiquitous property of certain portions of the central nervous system. In an extensive series of experiments (reviewed by Groves & Thompson, 1970) these authors distinguished a system of arousal neurons in the medial portions of the spinal cord. This system of neurons in turn converges with another more laterally placed set of decrementing neurons onto a final common path that habituates and dishabituates much as does the motor behavior in which these neural systems are involved. There is every reason to believe that the rostral extension into the mesencephalic brainstem of this column of medially placed cells accounts for the well-documented arousal effects of stimulations of the reticular formation (see Lindsley, 1961; Magoun, 1958 for review). Such effects are obtained even more rostrally in the diencephalon in a continuation of this neuron system into the hypothalamus where episodes of fighting and fleeing are produced by electrical or chemical stimulation of the so-called "defense" region of the hypothalamus.

These behaviors have been shown to be related to the orienting reaction. Abrahams and Hilton (1958) and Abrahams et al. (1964) found that in attempting to produce a defense response by stimulation of the hypothalamus, at first a low degree of arousal occurred, indicated by pupil dilation and postural alerting. Only when the level of stimulation was increased and maintained for a few seconds, did hissing, snarling, running, and piloerection occur. In the later study, alerting behaviors

were measured in greater detail, and during mild stimulation the authors observed changes in pupil dilation, head movements, pricking the ears, respiration, and blood flow. These same changes were also recorded during responses to simple auditory, visual, or cutaneous stimuli, in the absence of hypothalamic stimulation. Since these physiological changes are the same as those observed in all orienting responses, the defense reaction could therefore be considered in part to be due to an increase in arousal.

Converging on these hypothalamic structures are two reciprocally acting circuits regulating arousal. These circuits center on the amygdala (see the more extensive review by Pribram & McGuinness, 1975). One of these circuits involves the dorsolateral frontal cortex and is excitatory since resections of this structure **invariably** eliminate visceral autonomic orienting responses. The other, opposite in function, is more likely related to the orbitofrontal cortex which has been shown to be the rostral pole of an extensive inhibitory pathway (Kaada, Pribram, & Epstein, 1949; Wall & Davis, 1951; Pribram, 1961; Skinner & Lindsley, 1973; Sauerland & Clemente, 1973). These data relate to the descriptions of the behavior of amygdalotomized animals (Pribram & Bagshaw, 1953) which focused on the fact that they were tame, unresponsive to threat, and nonaggressive. However, the opposite finding was occasionally observed (e.g., Rosvold, Mirsky, & Pribram, 1954) and more recent behavioral studies by Ursin and Kaada (1960) using restricted lesions and electrical stimulations have confirmed the suggestion that at least two more or less reciprocal systems can be identified in the amygdala.

Such reciprocal innervation allows sensitive modulation (tuning) of the arousal mechanism. This is in accord with evidence on other control functions of the amygdala and related structures. Thus, injections of carbachol into the appropriate hypothalamic site will initiate drinking; such injections into the amygdala have no effect unless the animal is already drinking, in which case the amount of drinking becomes proportional to the amount of carbachol injected in an exquisitely accurate relationship (Russell, Singer, Flanagan, Stone, & Russell, 1968). Extrapolating to the issue before us, the frontoamygdala influence can be conceived as a finely tuned determinant controlling visceromotoric arousal initiated by the hypothalamic mechanism during orienting. It is as if in the absence of the frontoamygdala systems, the animal would fail to control its drinking behavior: Once started it would drink under circumstances in which others would stop. This is exactly what happens—and more. Both eating and drinking are controlled in this fashion—and not only their cessation, but also their initiation (Fuller, Rosvold, & Pribram, 1957).

A clue to what these controls on arousal accomplish comes from the finding that despite an essentially normal reactivity to shock, the amygdalectomized subjects have fewer spontaneous GSRs during the shock sessions, suggesting a change in base level (Bagshaw & Pribram, 1968). That baseline changes do occur after amygdala lesions was demonstrated directly in sustained chronic changes in the response measures (Pribram, Reitz, McNeil, & Spevack, 1979) and indirectly by various studies which showed that although behavioral and some electrocortical responses appeared to be normal during orienting (Schwartzbaum, Wilson, & Morrissette, 1961; Bagshaw & Benzies, 1968) the background level of these responses is lower than for controls. Ear flicking is practically absent during interstimulus intervals, and it takes less time for the lesioned animals to attain a criterion of slow wave activity in the EEG (Bagshaw & Benzies, 1968) in the preparatory phase of the experiment. Electromyographic responses occur with normal latency, although their amplitude is considerably reduced (Pribram, Reitz, McNeil, & Spevack, 1979). These results indicate that at the forebrain level, just as at the spinal level in Groves and Thompson's experiments (1970), arousal and decrementing systems converge to produce orienting, habituation, and dishabituation.

Perhaps the most striking chronic psychophysiological change to follow amygdalectomy was the finding of a paradoxically elevated basal heart rate (Bagshaw & Benzies, 1968; Pribram et al., 1979). This puzzled us considerably and made data analysis difficult, since operated and control monkeys had to be matched for basal rate, and it had to be shown that no ceiling effect was operating. We wondered whether arousal as a concept was in fact untenable in the face of a lack of evidence for orienting coupled with an elevated heart rate. Experimental results obtained by Elliott et al. (1970) and his analysis clarified the issues. He expected an elevated tonic heart rate to accompany arousal (defined as a response to collative variables such as surprise, uncertainty, novelty, and complexity of input much as we have defined them here) but as he was recording tonic rather than phasic changes he found the opposite: "These collative variables either had no effect on tonic heart rate or they had an effect (deceleratory) opposite to expectations; but response factors and incentive factors (reinforcing consequences) had strong accelerating effects [p. 185]." Thus, arousal as noted earlier is accompanied primarily by no change or immediately followed by tonic heart rate deceleration, which is indicative of activation. In short, our monkeys with absent arousal reactions showing an elevated chronic heart rate appeared to be working with considerable effort. In accord with the psychophysiological data on humans, such elevated tonic heart

rate is manifest when the situation demands effort on the part of the organism. Our observations suggest that without such expenditure of effort the amygdalectomized monkeys tend readily to fall asleep.

We therefore interpret the effects of amygdectomy as follows: Because the specific controls on arousal are removed, arousal results not in the registration of the situation by altering the neuronal model, but in immediate reflexive distraction. This increased distractibility evokes a defensive effort to cope with the situation. The defense reaction is characterized by an attempt to shut off further input (Pribram, 1969), an effect inferred from neurophysiological evidence of control over input. The effort is reflected in an elevated heart rate and other changes in chronic variables indicative of a continuing defense against impending breakdown in the coordination involved in maintaining a set in the face of distraction. This interpretation is borne out by the results of an experiment in which infant kittens were raised in isolation; when examined at the age of six months, their visceromotor and endocrine reactivity in orienting experiments was similar to that of amygdalectomized subjects. They had not learned to cope with situations and thus showed the "defensive" syndrome suggestive of considerable effort (Konrad & Bagshaw, 1970).

In summary, studies relating brain function and the orienting reaction to sensory input have pointed to the presence of a system of neurons responding to the amount of input by maintaining or incrementing their activity. This core system of neurons extends from the spinal cord through the brainstem reticular formation, including hypothalamic sites, and lies in close proximity to those responsible for the engenderment of visceromotor responses. By way of its diffuse connections, this system is responsible for the ubiquitous arousal responses recorded throughout the brain concomitant with orienting. Forebrain control over this core brain arousal system is exerted by reciprocal facilitatory and inhibitory circuits centered on the amygdala. These circuits control the onset and duration of neural arousal much as they control the onset and duration of visceromotor and appetitive responses.

Our interpretation of the relationship between the lack of visceromotor responses to orienting and the failure to habituate behaviorally has led us to suggest that a deficiency is produced in the ubiquitous central mechanism by which organisms register input. When such failure in registration occurs, the organism's nervous system is temporarily swamped by the arousing input and reacts defensively to shut out all further input. This leads to automatisms. Our interpretation fits the clinical picture of the amnesic states (*deja* and *jamais vue*) and the automatisms occurring during psychomotor seizures produced by

epileptic lesions in the region of the amygdala. There is also considerable congruity between this interpretation and those of Mednick and Schulzinger (1968) and of Venables (Gruzelier & Venables, 1972) in their report of two classes (GSR responders and nonresponders) of patients diagnosed as schizophrenics. However, the interpretation also suffers from the difficulties that plague understanding of these clinical syndromes: How do disturbances of registration in immediate awareness influence subsequent retrieval? More of this in the following sections.

B. Activation and the Control of Attention: The Contingent Negative Variation and Transcortical Negative Variations

As noted earlier, activation is marked by a period of delay between either (a) an arousal to input and the performance of an act, or (b) action sequences. As the animal (or human) is intending to do something about the current situation his behavior is arrested.

The simplest situation demanding serially organized responses is one in which two successive input signals are separated by an interval. The first input signals the organism to become ready to make a response to the second, which determines the outcome. As noted above, a large body of data has been gathered in this situation, using slow changes in brain electrical activity such as the *contingent negative variation* (CNV) (Walter, Cooper, Aldridge, McCallum, & Winter, 1964) and tonic changes in heart rate (Lacey & Lacey, 1970).

The CNV was originally proposed to reflect an expectancy developed when a specific response was contingent on awaiting the second of two stimuli. This would suggest that the CNV reflects another central event indicating that an input is about to be matched to the organism's neuronal model. However, other workers suggested that the negative shift in potential reflected intended motor activity (e.g., Kornhuber & Deecke, 1965; Vaughan, Costa, & Ritter, 1968). Still others (Weinberg, 1972; Donchin, Gerbrandt, Leifer, & Tucker, 1972) demonstrated that a CNV occurs whether or not an overt motor or even a discriminative response is required, provided some set or expectancy is built into the situation. Such sets do, of course, demand postural motor readiness. Weinberg (1972), for instance, has shown that in man the CNV continues until feedback from the consequences of reinforcement of the response occurs. Similar evidence has been obtained in monkeys (Pribram, Spinelli, & Kamback, 1967).

In a review of the CNV literature, Tecce (1972) suggests that three types of negative potentials interact depending upon the demands of the

experiment: (a) CNV due to expectant attentional processes; (b) the motor readiness potential signaling intention to act; and (c) more or less spontaneous shifts whose occurrence cannot be attributed to specific task situations. This classification, though consonant with results from a series of animal studies (Donchin, Otto, Gerbrandt, & Pribram, 1971, 1973), does not indicate the full diversity of the CNV. Recordings were made from several cortical locations under a variety of vigilance conditions. These studies showed that sites which produced *transcortical negative variations* (TNVs) depended upon the type of vigilance task. Thus, frontal TNVs are recorded only early in a task and when the task is changed; motor negative potentials are recorded only in anticipation of the necessity to make an overt response; postcentral negative potentials are largest when the organism must hold a response (continuously depress a lever) until a signal to release it occurs; and special sensory systems respond to their specific inputs (Pribram, 1971). The TNV appears to be an indication of either arousal or activation of the brain tissue from which it is recorded.

These data are amply confirmed by a recent study on humans (Gaillard, 1977) in which preparation was compared to expectancy in three detection tasks, one involving speed, another accuracy, and the third, detection, but no response. The frontal leads mirrored the task expectancy, whereas the posterior leads were affected by the task demands. The speed condition produced maximal CNV shifts in the parietal leads, whereas no parietal CNV occurred in the no response condition.

Sustained, tonic changes in potential have also been noted in subcortical negative potential shifts recorded in animals by Rebert (1972, 1973a,b) and in man by Grey Walter (1967) and by Haider (1970). It is yet too early to characterize the meaning of such shifts for every location, but in general, it appears that negativity develops whenever a portion of brain tissue is maintaining a readiness for processing. This conclusion has also been reached by Hillyard (1973) in an analysis of the CNV and human behavior. Hillyard also noted, in line with our analysis, that brainstem controls on overall cerebral negativity exist. We therefore will distinguish between the term TNV (multiple local readiness of cerebral tissues) and CNV (controls on these local potential shifts).

At the end of the negativity, if and when the organism actually begins to do something, a sharp positive deflection is usually observed, and this positivity has been related to consummatory behavior (Clemente, Serman, & Wyrwicke, 1964) and to a sharp increase in power both in the alpha (8-12 Hz) and theta (4-8 Hz) ranges (Grandstaff, 1969) in the visual cortex.

Preliminary evidence (Rebert, 1972; Walter, 1967) suggests that a

source controlling CNVs indicative of activation may be located somewhere in the region of the dorsal thalamus and basal ganglia of the forebrain because the polarity of slow variations in brain potential is similar in hypothalamic and cortical leads but shows a reversal in the depths of the brain. There is a mechanism which converges onto the far-lateral hypothalamic region which is not composed of cells but of fiber tracts such as the median forebrain bundle and others perpendicular to it. The data, from the studies recording deep-lying CNVs, suggest the hypothesis that we look for the control of the activation process in the basal ganglia which give rise to many of the fiber tracts that make up the far lateral hypothalamic crossroads. Recently completed studies substantially support this hypothesis.

In a series of studies employing multiple small stereotactic lesions in the globus pallidus, putamen and caudate nucleus, Denny-Brown and Yanagisawa (1976) report their findings with the following summary: "What, then, is absent? It would appear to be the activating 'set' or 'pump primer' for a certain act, the preparation of the mechanism preparatory to a motor performance oriented to the environment [p. 41]." They also note a particular type of ramp discharge in electrical activity in putamen neurons (DeLong & Strick, 1974) which precedes the motor performance at every stage. They suggest this operates as a facilitatory discharge which establishes a "climate" for performance.

They further suggest "the basal ganglia have all the aspects of a 'clearing house' that accumulates samples of ongoing cortical projected activity and, on a competitive basis, can facilitate any one and suppress all others [p. 45]." This indicates that part of this system relates to an ability to transfer attention from one type of stimulus to another and maintain that attentional set.

In addition, studies on animal and human patients with basal ganglia lesions (Bowen, 1976) could be interpreted as indicating an inability to maintain attention. Patients showed deficits in a range of perceptual and cognitive tasks, including orientation for both internal and external space, concept formation tasks, formation of a set to respond, and short-term memory in all modalities. As these tasks are unrelated to one another in the cognitive domain, we suggest the deficit is due to problems of maintaining readiness (or set) to complete a task.

C. Effort in the Integration of Arousal and Activation

The data on animal behavior following hippocampectomy strongly imply that this structure is critical in the regulation of the arousal and activation modes. Subjects with bilateral hippocampectomy tend to

show a percentage of reactivity and amplitude of the GSR opposite to that observed in the nonresponding amygdalectomized monkeys (Figures 3.1 and 3.2) in the ordinary orienting paradigm. In addition, the phasic skin response terminates considerably more rapidly in hippocampectomized subjects than in controls (Figure 3.3). It appears from this that hippocampectomized monkeys (and amygdalectomized hyperresponders) reequilibrate more rapidly than normal subjects whose slower GSR recovery may indicate a more prolonged processing time. As we shall see, this finding is consistent with other data that show impaired processing of the disequilibrium produced by a mismatch of input to the neuronal model as a result of hippocampectomy.

A further change is that such subjects show delayed or absent orienting reactions when thoroughly occupied in performing some other task

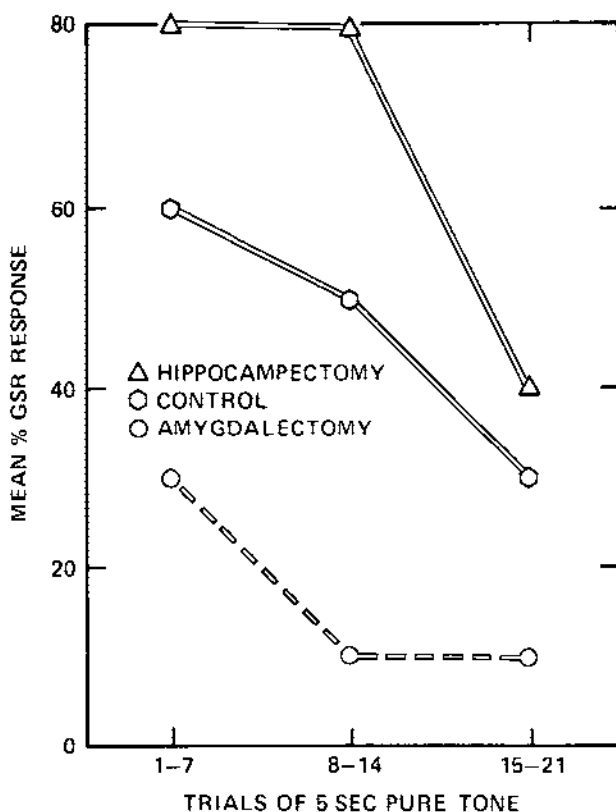


FIGURE 3.1. Curves for a more detailed analysis of the first 21 trials (split into 7-trial blocks) or percentage of galvanic skin response (GSR) to a 5-sec tone for the amygdallectomized, hippocampectomized, and unoperated monkeys.

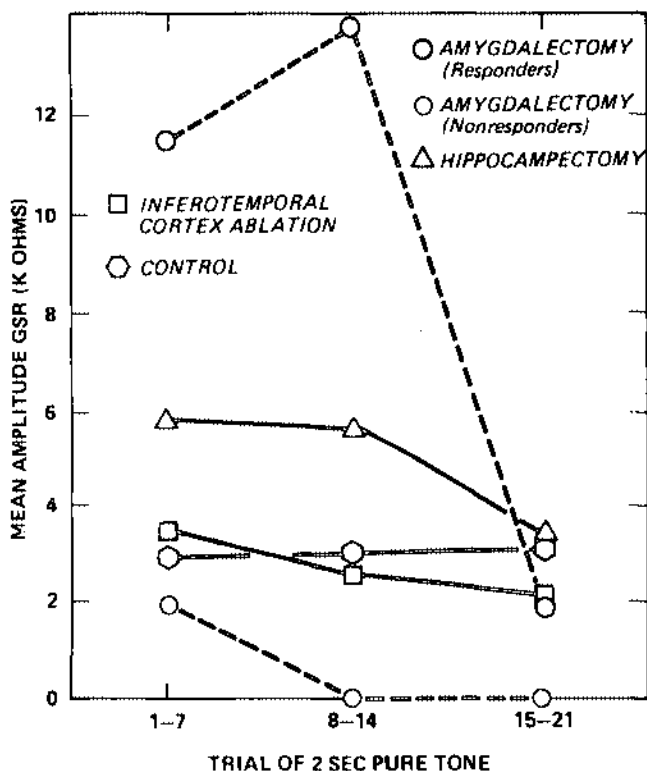


FIGURE 3.2. Group mean amplitude for galvanic skin response (GSR) to tone on the first 21 trials showing the bimodal distribution of the amygdalectomized monkeys when compared with normal (control) and with two other brain-lesioned groups of monkeys: inferotemporal cortex resection and hippocampectomy.

(Crowne & Riddell, 1969; Kimble, Bagshaw, & Pribram, 1965; Rappelson, Isaacson, & Douglas, 1965; Riddell, Rothblat, & Wilson, 1969; Wicklegren & Isaacson, 1963). In short, these animals appear to be abnormally intractable.

But in some situations this appearance of intractability is restricted to the overt responses of the organism, not to orienting per se. Douglas and Pribram (1969) used distractors in a task in which responses were required to each of two successive signals. Hippocampectomized monkeys initially responded much as controls did by overtly manipulating the distractors, which were presented between the two signals, increasing the time between the two required responses. In contrast to the behavior of the controls, who habituated manipulation of the distractors and the interresponse time, the hippocampectomized group showed

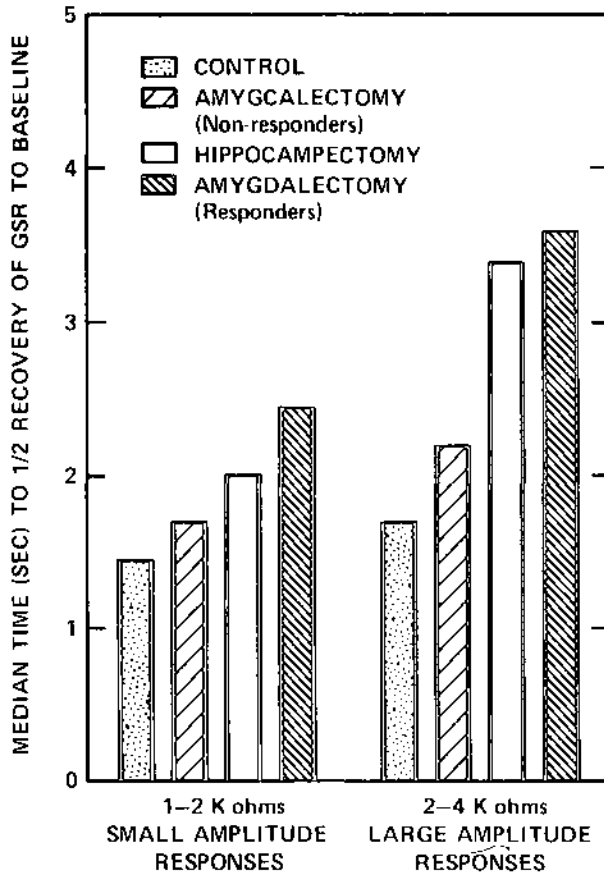


FIGURE 3.3. Bar graphs showing the time taken to attain half recovery to baseline of the viscerosomatic perturbation measured as an electrodermal response (galvanic skin response, GSR). Small, 1-2 Kohms, and large, 2-4 Kohms, perturbations are treated separately since amplitude of response has an obvious effect on recovery time.

decrementing only of the manipulations—their interresponse time failed to habituate at all. In this situation, hippocampectomized monkeys continue to be **perceptually** distractible while becoming behaviorally habituated and indistractable (Figure 3.4). This result is identical to that obtained in man with medial temporal lesions: Instrumental behavior can to a considerable extent be shaped by task experience, but verbal reports of the subjective aspects of experience fail to indicate prior acquaintance with the situation (Milner, 1958).

The dissociation between habituation of perceptual responses and habituation involving somatomotor performance appears to be part of a

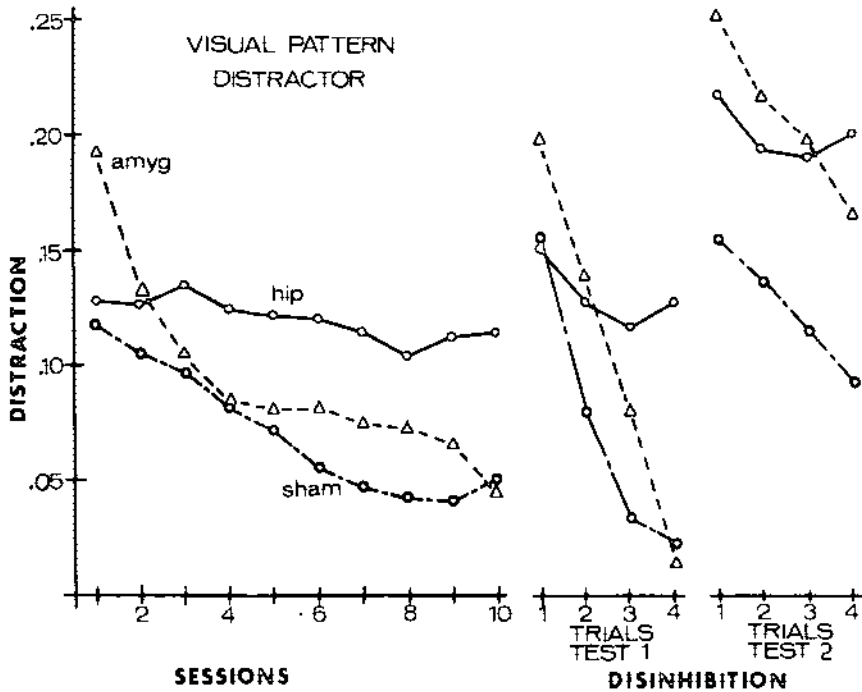


FIGURE 3.4. Distraction with visual pattern stimulus as distractor. (Abbreviations: sham = sham-operated subjects; amyg = amygdalotomized monkeys; hip = hippocampectomized animals.)

more general effect of hippocampal lesions, as it is manifest in other situations in which hippocampectomized monkeys are tested. In a discrimination reversal situation, extinction of previously learned behavior and acquisition of new responses were observed. In contrast to their controls, however, the monkeys with the hippocampal lesions remained at a chance level of performance for an inordinately long time (Pribram, Douglas, & Pribram, 1969). This effect was due to the "capture" of the behavior by a position bias during the 50% schedule of reinforcement—a bias hardly manifest in unoperated monkeys (Figure 3.5 and 3.6; Spevak & Pribram, 1973). This result suggested that a hierarchy of response sets was operative in the situation such that "observing" responses (indicative of attention) were relinquished when the probabilities of reinforcement ranged around the chance level.

Taken together, these experimental results suggest that interference with the hippocampal circuit reduces the organism to a state in which effort-demanding relationships between perception and action, between observing and instrumental responses, and between stimulus and re-

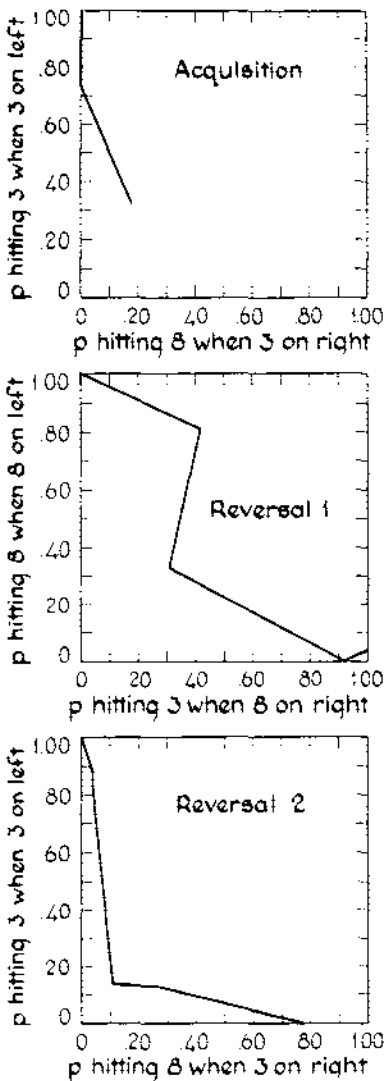


FIGURE 3.5 Individual curves for an intact monkey during discrimination and the first two reversals. (The curves were constructed by joining in temporal sequence points summarizing pattern-discrimination and position preference of the monkey for 50 trial sessions during pattern-discrimination and reversal training.) [From "A decisional analysis of the effects of limbic lesions in monkeys," by A. Spevack & K. H. Pribram, *Journal of Comparative and Physiological Psychology*, 1973, 82, 211-226. Copyright 1973 by the American Psychological Association. Reprinted by permission.]

sponse, are relinquished for more primitive relationships in which either input or output captures an aspect of the behavior of the organism without the coordinating intervention of central control operations. The mechanism by which the hippocampal circuit accomplishes this relationship has been elucidated to some extent by recordings of electrical activity from the hippocampus, both with micro- and macroelectrodes, and by precise electrical stimulations of selected parts of the hippocampal circuit.

The hippocampus with its three-layered cortex provides the best opportunity for observing unit activity responsible for the changes observed in gross electrical activity in repetitive situations. Vinogradova (1970) found that all neurons of the hippocampus habituate to repetition of a stimulus and dishabituate to any change in the stimulus configuration. But she distinguished two types of neurons, *A* and *I*: those activated (30–40%) and those inhibited (60%) by a stimulus, respectively.

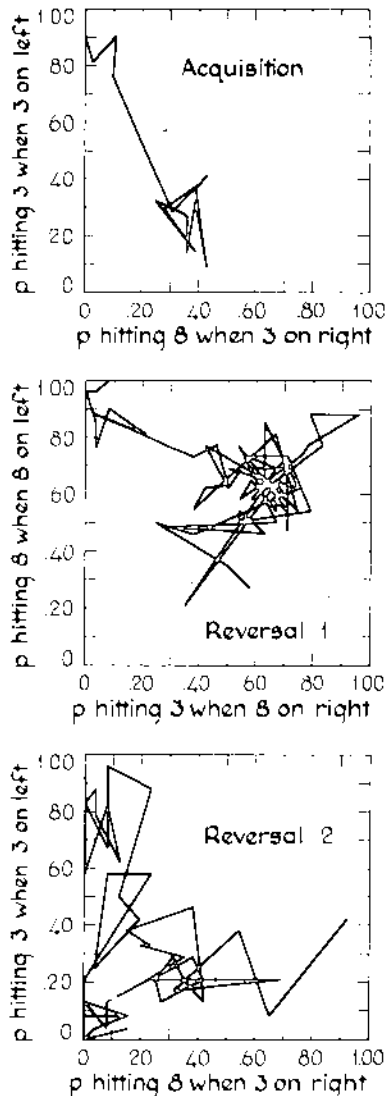


FIGURE 3.6. Individual curves for a hippocampectomized monkey during discrimination and the first two reversals (The curves were constructed by joining in temporal sequence points summarizing pattern-discrimination and position preference for the monkey for 50 trial sessions during pattern discrimination and reversal training.) [From "A Decisional Analysis of the effects of limbic lesions in monkeys," by A. Spevack & K. H. Pribram, *Journal of Comparative and Physiological Psychology*, 1973, 62, 211–226. Copyright 1973 by the American Psychological Association. Reprinted by permission.]

Habituation occurs by a progressively shortening response in the course of 16–20 repeated presentations. The averaged poststimulus histograms of the two classes are “mirror images of each other.”

Some important characteristics of hippocampal units are (a) the latencies of response to a stimulus do not change; (b) they are of the order of 100–1000 msec even initially; (c) in the ventral hippocampus (the only part present in primates, including man) stimuli must be of a minimum duration of from .5 to 1 sec to produce any noticeable change in the background activity; and (d) such facilitation persists up to 1 min after the cessation of the stimulus. These characteristics indicate a necessity for a long period of summation to precede hippocampal facilitation. Vinogradova (1970) interprets her findings as follows: “The duration of reactions in hippocampal neurones shows that the processes continue here long after the information processing is finished in all specific sensory structures, and in primary and secondary areas of the cortex as well. . . . As Gloor (1961) indicated, the quality of sensory information is almost erased in hippocampal neurones [pp. 114–115].”

These results are in accord with proposals previously put forward by Douglas and Pribram (1966). They suggested that the hippocampus constitutes part of an error (mismatch) evaluating mechanism which was conceived to process only the perturbations resulting from the mismatch among inputs (including those consequent on responses) (Pribram, 1971). Vinogradova is in agreement, therefore, in suggesting that precise sensory information is not involved. Further, she suggests a mechanism by which such processing can be achieved: “The hippocampus exerts a tonic inhibitory influence upon the reticular formation, blocking activity processes through the tonic discharge of its I-neurones when novelty is absent and registration is not needed. But when a stimulus which is not registered in the memory system appears, this inhibitory control is blocked (I-neurones become silent), arousal occurs, and the process of registration starts [p. 114].”

Lindsley has recently elaborated the mechanism by which the hippocampally controlled reticular formation can effect these changes in registration. Lindsley (Macadar, Chalupa, & Lindsley, 1974) in keeping with many other recent publications (e.g., Fibiger et al., 1973; Ungerstedt, 1974) has dissociated two systems of neurons that influence the hippocampal circuit. One system originates in the median raphé and associated structures of the mesencephalic reticular formation, the other originates more laterally in the locus coeruleus and other portions of the periaqueductal gray. Lindsley's findings were obtained by electrical stimulations of the appropriate structures in the mesencephalic reticular formation. Stimulations of the raphé mechanisms produced hippo-

campal desynchronization and at the same time a synchronization of the amygdala circuits. Taken together with Vinogradova's evidence, this suggests a reciprocal process by which the controls on arousal are maintained as long as hippocampal inhibition of the reticular formation is in progress—much as Vinogradova suggests. Only when a mismatch from the neuronal model is signaled to the reticular formation does this inhibitory control become loosened, producing hippocampal desynchronization and concomitant relaxation (synchronization) of the arousal functions of the amygdala circuits. Lindsley has found that often, though not always, such hippocampal desynchronization is accompanied by desynchronization of the sensorimotor projection systems, suggesting that registration, an alteration of the neuronal model of the cortical representation, is occurring. Note that in this formulation the term "registration" refers to a change in the neuronal model, thus a "registration in memory," a process that, as we shall see, requires effort. This use of the term registration must be distinguished from "registration in awareness" which, as noted earlier, is disrupted by interference with the amygdala circuits.

The second mechanism discerned by the Lindsley studies is the locus coeruleus system. This mechanism makes possible the "What is to be done?" reaction, the processing of response-produced inputs. When electrically stimulated, the mesencephalic portions of this mechanism initiate hippocampal rhythmic activity in the theta range of frequencies. Early studies (Green & Arduini, 1954) had uncovered the paradox that the desynchronization of the EEG recorded from the brain's convexity during activation was accompanied by synchronization in the recordings obtained from the hippocampus. Though such synchronization is not as obvious in records obtained in monkey and man, computer analysis has shown that it does occur and that it can be studied in the primate (Crowne, Konow, Drake, & Pribram, 1972). This synchronous rhythm is in the theta range (4–8 Hz) and has become the focus of a long series of studies.

Theta frequencies were first recorded from the hippocampus by Jung and Kornmuller in 1938. Since this discovery, theta has been implicated in orienting behavior (Green and Arduini, 1954; Grastyan, 1959; Grastyan, Lissak, Madarsz, & Donhoffer, 1959) and in intended movement, even when tested under curare (Dalton & Black, 1968; Black & Young, 1972; Black, Young, & Batenchuck, 1970). Vanderwolf and his associates (Bland & Vanderwolf, 1972a,b; Vanderwolf, 1969, 1971; Whishaw, Bland, & Vanderwolf, 1972) noted that theta activity occurred almost exclusively when animals (rats) were making voluntary movements.

Brenner (1970) analyzed the changes in theta activity along three dimensions: (a) an increase or decrease in the total amount of power (amplitude in millivolts) in the theta range; (b) a narrowing or broadening of the range of energy or power around a particular frequency; (c) the specific peak frequency. An increase in power of the whole theta range relates to viscerautonomic arousal and a decrease in power to somatomotor readiness. The changes in bandwidth seem to be dependent upon whether the animal is performing in an intake (categorization) or a rejection (problem solving) mode; and thus relate to **effort** and the contents of awareness.

V. Neurochemical Mechanisms In Attention

Currently, a body of data has accumulated relating a variety of brain peptides, many of them derivatives of adrenocorticotrophic hormone (ACTH), to a variety of behaviors. Interestingly, the behaviors that have become involved in brain peptide research are to a large extent the same as those involved initially in amygdala research and then shown to be dependent on hypothalamic, basal ganglia, and hippocampal function as well. Thus the neural organization of the mechanisms of arousal, activation, and effort delineated by neurobehavioral and psychophysiological techniques may well be relevant to the analysis of the relationship between neurochemical and behavioral processes.

A. Brain Amines in Arousal and Activation

Perhaps the easiest place to start is the by now well established and dramatic finding of a dopaminergic nigrostriatal system (Fibiger, Phillips, & Clouston, 1973; Ungerstedt, 1974) which has already been discussed. The evidence has repeatedly been reviewed to the effect that dopamine is involved in the maintenance of postural readiness and motivational activation (Matthyse, 1974; Snyder, 1974). It is also known (e.g., King & Hoebel, 1968) that assertive behavior such as predatory aggression depends on the activation of a cholinergic mechanism. Thus, it is likely that the dopamine fibers interdigitate a cholinergic matrix (Fuxe, 1977) to determine the activation level of the nervous system and the readiness of the organism.

Two other by now well known neurochemical systems are those involving serotonin and norepinephrine. A large amount of research (e.g., reviews by Jouvet, 1974; Barchas, Ciaranello, Stoke, Brodie, & Hamburg, 1972) has related these substances to the phases of sleep: serotonin to ordinary (slow-wave) sleep and norepinephrine to paradoxical (rapid-

eye-movement, or REM) sleep during which much dreaming occurs. The relationship between serotonergic and norepinephrinergic mechanisms and the amygdala, seems to be similar to that between acetylcholine (ACh) and dopamine, and the striatum of the basal ganglia. Serotonergic and norepinephrinergic systems of fibers densely innervate the amygdala, the norepinephrinergic systems interdigitating a serotonergic matrix (see Pribram and Isaacson, 1976, for review).

The regulation of sleep by the amygdala has not been quantitatively documented but sleep disturbances are commonplace immediately following amygdectomy, the animals often falling into a torpor from which they are difficult to rouse for several days to several weeks.

However, norepinephrine has been related to a behavioral function in which the amygdala is thoroughly implicated—the effects of reinforcing events (Stein, 1968). Norepinephrine has also been related to orienting and affective agonistic reactions. Once again a phasic response to novelty—sensed against a background of familiarity—is norepinephrinergic, whereas “familiarity” in the guise of “territoriality” and “isolation” has been shown to some extent to be dependent on a serotonergic mechanism (see reviews by Reis, 1974; and Goldstein, 1974).

These data suggest that norepinephrine acts by modulating a serotonergic substrate (which is determining one or another basic condition of the organism) to produce paradoxical sleep, reinforcement, orienting to novelty, and perhaps other behaviorally relevant neural events that interrupt an ongoing state. The data are not as clearly supportive of this suggestion as those that relate acetylcholine to an assertive state that is modulated by the activity of dopamine to produce specific readinesses. Nonetheless, as a first approximation to the data at hand, let us hold these possible neurochemical relations in mind as a tentative model with which to analyze the mass of evidence on the behavioral neurochemistry of the polypeptides.

B. Neuropeptides and the Effort—Comfort Mechanism

The neurochemical evidence on ACTH-related peptides leads directly to the hypothesis that they are involved in the hippocampal mechanism. To begin with, Bohus (1976) and McEwen, Gerlach, and Micco (1976) have shown that the hippocampal circuit (hippocampus and septum) is the brain site most involved in the selective uptake of adrenal cortical steroids. As McEwen states:

It is only quite recently that we have come to appreciate the role of the entire limbic brain, and not just the hypothalamus, in these endocrine-brain interactions.

Our own involvement in this revelation arose from studies of the fate of injected radioactive adrenal steroids, particularly corticosterone, when they

entered the brain from the blood. These studies were begun, under the impetus of recent advances in molecular biology of steroid hormone action, to look for intracellular hormone receptors in brain tissue. We expected to find such putative receptors in the hypothalamus, where effects of adrenal steroids on ACTH secretion have been demonstrated (Davidson *et al.* 1968; Grimm & Kendall, 1968). Much to our surprise, the brain region which binds the most corticosterone is not the hypothalamus but the hippocampus [McEwen *et al.*, 1976, p. 285].

Thus the receptors of adrenal cortical hormones can set the neural state which becomes modulated by ACTH-related peptides. Evidence that such modulation of a corticosterone determined state involves the hippocampus has been presented by van Wimersma, Greidanus, and de Wied (1977).

Second, as previously noted, the hippocampal circuit functions to coordinate arousal (phasic response to input) and activation (tonic readiness to respond). Thus, in any complex behavioral situation, coordination would be influenced by manipulations of this circuit—and a host of apparently conflicting results might be obtained with very slight changes in the conditions of the experiment. (The best known of such slight changes is the one-way versus two-way conditioned avoidance task, see Pribram, Poppen, & Bagshaw, 1966; and van Wimersma *et al.*, 1977.)

Further, effects on phasic and tonic processes (arousal and activation) as well as on their coordination (effort) would be expected. This expectation is borne out in the catalogue of effects of manipulations of ACTH related peptides: extinction of two-way but not one-way avoidance (de Wied, 1974); interference with passive avoidance (Levine & Jones, 1965); interference with learned taste avoidance (the Garcia effect—Levine, 1977); interference with discrimination reversal (Sandman, George, Walker, Nolan, & Kastin, 1977); facilitation of memory consolidation (van Wimersma *et al.*, 1977); facilitation of exploratory behavior and conditioning (Endroczi, 1972, 1977).

Just as in the case of manipulations of hippocampal activity, **ongoing** behavioral activity (memory consolidation, exploratory behavior) is facilitated while any **change** in behavior (two-way shuttle, passive avoidance, learned taste aversion, discrimination reversal) is interfered with. This appears initially as tilting the bias toward readiness. But as Pribram and Isaacson (1976) show for hippocampal function, and Sandman's group conclude (see Miller, Sandman, & Kastin, 1977), such an interpretation does not hold up. In the case of hippocampal research, the initial formulation stated that after hippocampal resections, animals could not inhibit their responses (McCleary, 1961). This interpretation

founded when such animals were shown to perform well in go-no-go alternation tasks (Pribram & Isaacson, 1976; Mahut, 1972) and that they could withhold behavioral responses despite an increase in reaction time when distractors were presented (Douglas & Pribram, 1969).

The most cogent analysis has been performed on discrimination reversals. Isaacson, Nonneman, & Schwartz (1968) and Nonneman and Isaacson (1973) have shown that reversal learning encompasses three stages: Extinction of the previously correct response, reversion to a position habit, and acquisition of the currently correct response. Pribram, Douglas, and Pribram (1969) and Spevak and Pribram (1973) have shown that hippocampally lesioned monkeys are intact with regard to both the extinction and the new acquisition phases of the reversal training experience. However, such monkeys seem to become "stuck" in the 50% reinforcement phase or in position response patterns. In short, the monkeys' behavior seems to be taken over by a relatively low variable interval schedule of reinforcement and they fail to "make the effort" to "pay attention" to the cues which would gain them a higher rate of reward. Champney, Sahley, and Sandeman (1977) have shown ACTH-related peptides to operate on just this aspect of the reversal experience—and, in fact, have shown interactions with sex differences.

Finally, we note that the ACTH-related peptides, the enkephalins, are endorphins—endogenous hormones that have morphinelike effects and in fact act as ligands on morphine receptors. These neuropeptides, and the hippocampal circuit in which they are operative, function therefore to modulate an effort-comfort dimension of experience and behavior.

Evidence such as this makes highly plausible the hypothesis that ACTH-related peptides operate on the hippocampal circuit and therefore the "effort" process. But there is more. Strand, Cayer, Gonzales, and Stoboy (1977) present direct evidence that muscle fatigue is reduced by ACTH-related neuropeptides and that this effect must be central. Until this study, the only evidence available on metabolic shifts due to the effort of paying attention came from the Berdina et al. (1972) study reviewed in the preceding section. It now appears that these peripheral anaerobic shifts affecting muscle tonicity may be a reflection of central processing modulated by ACTH neuropeptides.

V. Conclusion: Emotion and Motivation in Attention

Beginning with the work of Claude Bernard (1858), Karplus and Kreidel (1909) and Cannon (1929), the corebrain stem has been known to contain the major control mechanisms for visceromotoric (homeosta-

tic) regulations. As reviewed in Section IV, it became evident that these controls often involved reciprocally operating processes: those that stop behavior because satiety has been achieved and those that maintain appetitive behavior (see e.g., Grossman, 1966; and Pribram, 1971, for summaries). Feeding, for instance, is maintained during activity recorded from electrodes placed in the far lateral region of the hypothalamus whereas satiety is signaled by excitation of cells in its ventromedial nucleus. These go and stop mechanisms are multiply interlinked both centrally and by their peripheral effects; thus the homeostatic regulations in their totality are complex (Brobeck, 1948). Nonetheless, the reciprocal mechanisms can be determined to be at the root of the process. Furthermore, as noted earlier, electrical excitation of the satiety mechanisms has been shown to produce not only cessation of behavior but, at somewhat higher intensity, phasic arousal, and with even higher intensities, emotional behavior such as rage (Abrahams & Hilton, 1958; Abrahams et al., 1964). As we noted in Section IV these psychophysiological and behavioral manifestations characterize an entire brain system with connections to the medial hypothalamus. This system involves the amygdala and frontal cortex.

Further, we also noted that the far lateral system has interesting ramifications. At the hypothalamic level it is essentially devoid of cells and is mainly a crossroads of fiber tracts. The behavioral correlates of the system must therefore stem from the cells of origin of these fiber tracts. Recent cytochemical evidence (Ungerstedt, 1974) showed that the largest of the tracts in the crossroads was the nigrostriatal pathway which composes the prime dopaminergic system in the brain. Psychopharmacological studies (Fibiger, Phillips, & Clouston, 1973; Teitelbaum & Epstein, 1962) then demonstrated that antidopaminergic drugs would almost completely replicate the syndrome (aphagia which can be overcome under special conditions) produced by lesions of the far-lateral hypothalamic region. These results indicate that the appetitive behavior characterizing the functions of the far lateral system is largely due to involvement of the basal ganglia, structures known from clinical observation and other experiments to be also involved in the maintenance of postural and perceptual sets (Denny-Brown & Yanagisawa, 1976).

Taken together, these various experimental results have distinguished two neural systems, one clearly related to phasic arousal and emotional reactivity and the other to readiness and the maintenance of set and appetitive behaviors. As we reviewed in Section IV, there is further evidence that the readiness system is the substrate of psychophysiological tonic activation as defined in this chapter.

In short, these studies and the additional neurochemical evidence reviewed in Section V define separate brain systems to operate in emotional and motivational processes. Emotion is thus related to a phasic arousal system and motivation to a readiness, tonic activation system. The foregoing analysis and review of evidence indicates that these are systems in which neurochemical events determine to a large extent the behavioral functions that are regulated by these structures.

Regulation is in part affected by the establishment, through central receptor sensitivities, of neural representations of peripheral endocrine processes, and by direct influences on these representations of centrally active neurochemical substances. Among the many relationships between endocrines and central sensitivities, some were singled out as providing sufficient evidence that a systemization might be attempted. Others, such as the possible central effect of insulin, or the special sensitivity of the amygdala to sex hormones, have not been included, although they cannot be ignored in any future attempt at synthesis.

At the moment three classes of systems are discernible. One class determines specific neuromuscular and neurosensory readinesses. A second deals with the momentary cessations of ongoing behavior, cessations due to interrupting distractors, the intervention of satiety, or the recurrence of reinforcing events. The third class of systems coordinates the readinesses of the organism with the processes that lead to their momentary suspension.

The proposal was made that states of specific readiness were due to a cholinergic mechanism operated upon (i.e., modulated by), dopaminergic systems. The basal ganglia are the major gross forebrain embodiments of a readiness mechanism.

The amygdala is the gross forebrain locus upon which the systems that deal with momentary cessation of behavior and the concomitant emotional reactions, such as arousal (interest) and upset, converge. Neurochemically, these systems are posited to be basically serotonergic with norepinephrinergetic operators modulating the basic serotonergic state.

Finally, a coordinating effort-comfort determining mechanism was discerned whose forebrain extension lies within the hippocampal circuit. The neurochemical constitution of this class of systems is hormonal with neuropeptides operating on the hormonally induced neural state to regulate behavior. Corticosteroids and ACTH-related neuropeptides are examples of the functions of this third class of systems.

We have identified emotional processes as rooted in the phasic arousal mechanisms discussed here and distinguished them from motivational processes rooted in the readiness mechanisms. Thus the neurochemical

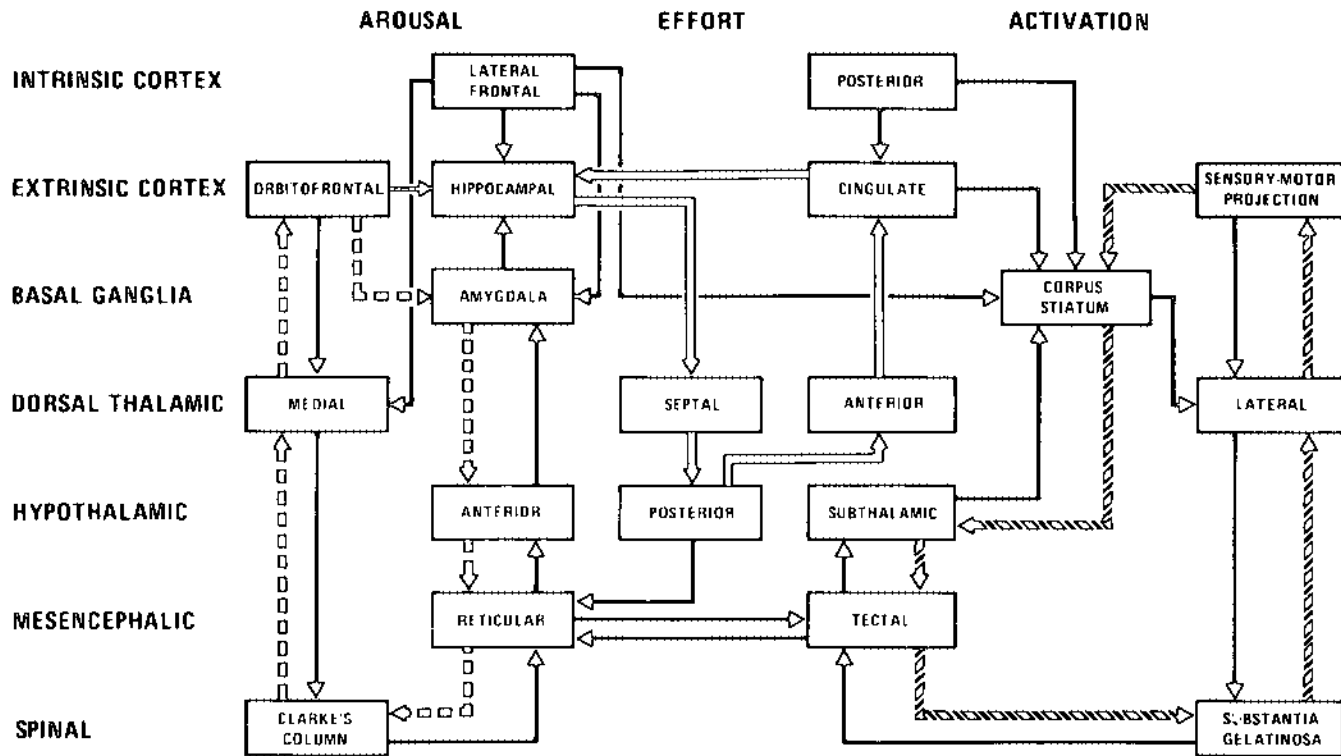


FIGURE 3.7. A highly oversimplified diagram of the connections involved in the arousal (amygdala), activation (basal ganglia), and effort (hippocampal) circuits.

analysis undertaken here is relevant to both emotion and motivation. The analysis would predict that neuropeptides would be only indirectly involved in the regulation of emotion (affect) and motivation. Only when emotional and motivational processes need to be coordinated would neuropeptide manipulations show an effect. Emotion and affect are found to be minimally influenced by ACTH-related compounds in man (Ehrensing & Kastin, 1977). Conflict producing tasks such as passive avoidance (Levine & Jones, 1970), learned taste aversion (Levine, 1977), two-way shuttles (de Wied, 1974, 1977), and frustrative non-reward (Grey, 1977) are the instruments of choice for demonstrating the effects of neuropeptides. One-way shuttles and simple punishments show either no effect or a mild facilitation of the reinforcing process.

A summary diagram of the three systems is presented in Figure 3.7. Thus, emotional and motivational controls on attention have been found to operate via three neuroanatomical, neurophysiological, and neurochemical systems. One such system deals with arousal defined as a phasic response to input. The second system deals with activation, a readiness to respond. The third system coordinates arousal and activation along an effort-comfort dimension. Neurophysiological and neurobehavioral evidence has been reviewed which link these systems to emotion and motivation and delineate their influence on attention. Psychophysiological evidence was adduced to show how these attentional processes operate during categorizing and reasoning. Attention thus becomes the central process that links emotion and motivation to cognitive operations.

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